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Growth correlations in maize seedlings

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GROWTH CORRELATIONS IN MAIZE SEEDLINGS

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INTRODUCTION

Growth correlation is the term used to designate the interaction of parts and organs during the course of plant development. Correlation is based upon competition for the available food materials, particularly for available proteins. Florists, for example, remove the axillary buds of Chrysanthemums to reduce competition with the apical bud, and obtain a larger flower. Or they may cut away the apical bud to remove its inhibiting action on the axillary buds. Orchard and landscape pruning practices are based upon correlative development. These practical applications of growth correlation have been established through years of usage, but it is only within the past two decades that the underlying principles of correlations have been intensively studied.

Striking responses, particularly in inhibiting the growth of buds and roots or of forcing the initiation of root tips have lead to the belief that growth hormones or auxins are correlation conditioners or carriers (76, 11, 25, 26). Three naturally occurring growth substances have been isolated from plant materials: auxin a and auxin b from green plants, and hetero-auxin from fungi. Auxin a, auxentriolic acid, has the chemical formula $C_{18}H_{32}O_5$. It is very unstable, but is apparently the most widely occurring auxin in plants. Auxin b, auxenolonic acid, having the chemical formula $C_{18}H_{30}O_4$,

is more stable than auxin a. Hetero-auxin, indole-acetic acid, which has the chemical formula $C_{10}H_9O_2N$, is the most stable of the three.

Inge and Loomis (32) observed a definite negative correlation between plumule and first internode growth in the development of maize seedlings. They also showed that roots at the coleoptile node were inhibited as long as active growth continued in the first internode. Exposure of the coleoptile to light inhibited the growth of the first internode and stimulated the production of foliage leaves by the plumule and the growth of nodal roots.

The present paper reports a continuation of these studies. It is concerned chiefly with the distribution of the growth of the maize seeding between plumule (usually including the coleoptile), the mesocotyl or first internode of the epicotyl (2, 14) and the roots, and of the relation of growth hormones to these correlative developments.

REVIEW OF PERTINENT LITERATURE

The first recorded careful study of growth correlations in plants was made by du Monceau in 1758 (76). He conceived the idea that correlation was brought about by the movement of two saps in the plant, one moving upward and the other downward. If the downward stream were intercepted by ringing, it caused swellings, callus, and even root formation at the point of interception. Du Monceau stressed the idea of root formation to the extent that he considered the swelling and callus to be of the nature of roots.

More than a hundred years later Darwin reported interesting experiments on the movement of plants in response to light (15). Experimenting with a grass coleoptile he demonstrated that a localized area at the tip was the region sensitive to light. He concluded that "when seedlings are freely exposed to a lateral light, some influence is transmitted from the upper to the lower part, causing the latter to bend". Darwin further observed that if the coleoptile tip were removed before exposure to light, no phototropic curvature resulted.

About thirty-five years later experiments of Boysen-Jensen (15) showed that the phototropic curvature was due to a growth differential on the light and dark sides of the coleoptile. He concluded from his observations that "conduction

of the stimulus in phototropic curvature takes place by the downward movement of a growth-promoting substance upon the back side of the coleoptile.

A few years later Paal, a German worker, repeated the experiments of Boysen-Jensen, and confirmed his findings. Paal observed that if the decapitated coleoptile tip was replaced on one side of the coleoptile stump, increased growth occurred on the side beneath the replaced tip, which resulted in a marked curvature of the coleoptile. This experiment proved that the "tip is the seat of the growth-regulating center". Paal referred to the correlation carrier that moved downward from the coleoptile tip as a growth hormone. He was the first to introduce the term growth hormone into botanical literature (76).

With the general acceptance of the growth hormone concept, and of growth hormones or auxins as "correlation carriers" in plant growth, many workers interested themselves in this new phase of plant physiology.

Perhaps no single internal factor influences growth correlation as much as auxins. It must not be thought, however, that they are the only internal substances effecting the development of plants. Bonner (11, 12) has listed inositol, biotin, vitamins B1 and B2, vitamin C and oestrone as accessory growth factors, necessary if growth is to take place. These are of course in addition to the primary carbohydrate and nitrogenous foods.

Very little is known about the formation of auxin in the plant. It appears to be stored in the endosperm of some seeds in the form of an inactive precursor substance (48), possibly an ester from which active growth substance may be obtained by the action of lipase (70). Navez (45) was able to obtain twice as much auxin from the tips of light grown Lupinus seedlings as from the tips of etiolated plants. He postulated that auxin formation is linked directly with photosynthesis. Avery, Burkholder and Creighton (5), working with shoots of Nicotiana under similar conditions, concluded that light had no effect on the production of auxin except indirectly through the synthesis of carbohydrates. Recently Van Overbeek (69) presented evidence that auxin is formed in excised pea root tips growing in vitro. Several workers have found that large quantities of auxin are produced in rapidly growing apical meristems (5, 6, 65, 54). The cells of the coleoptile tip seem to have an appropriate structure for the production of growth hormone (47).

The capacity of auxin to act as a correlation carrier in plant growth is conditioned in part by its response to light. This is especially true in the development of grass seedlings. It is only in seedlings that growth substance is found in the dark (73). Certain types of correlative growth result from the light inactivation or destruction of auxin in the coleoptile tip of the seedling (16). Katunskij (34, 35) found

that differentiation of cells of Avena seedlings depends upon the decrease in the content of growth substance caused by short periods of illumination. Burkholder and Johnson (17) have demonstrated that light destroys the activity of growth substance in the coleoptile tips of Zea and Avena. Many workers, however, have observed a physiological regeneration of the coleoptile tip several hours after exposure to light (24, 40, 59). It has been suggested that auxin is unstable in light, only when it is in combination with some cell constituent (57).

Grass seedings of Avena and Zea have been the favorite experimental plants in the study of growth hormones and growth correlations. Hormones occur in such minute quantities that no chemical method for their quantitative determination has been developed, and the coleoptile of the Avena seedling is used almost exclusively in demonstrating the presence of growth substances (15). Went (71) was the first to obtain auxin from the coleoptile tips of Avena. He found that auxin would diffuse from coleoptile tips into an agar block, and that the agar block placed unilaterally on a coleoptile stump caused a curvature proportional, within certain limits, to the concentration of growth substance within the block. Using this technique he devised a biological assay for the quantitative determination of growth hormones in plant materials.

Went's discovery made it possible to study the occurrence and to trace quantitatively the movement of the correlation carrier within the plant. With this method the presence

of growth substance has been demonstrated in many different plants and plant organs. According to F. A. F. C. Went (70), growth substance may be found throughout the plant kingdom, and probably no single species is without it.

Many workers have observed the polarized movement of auxin in the plant (70, 3, 23, 53, 60). Auxins usually move in a downward direction from the apex towards the base, and in their movement down the axis of the plant they stimulates cell elongation (5, 70, 73, 15), stimulate cambial activity (41, 52, 53, 56), and inhibit the development of lateral buds and shoots (25, 26, 39, 51, 54, 50). Auxins seem to be necessary for the initiation of roots on stems (22, 23), and probably also for the formation of branch roots on roots (61). Although auxins are necessary for the initiation of roots, they definitely inhibit root elongation (36, 61).

Correlative inhibition is by no means a rare phenomenon in plant development. Appleman(1) has shown that if potato "seed pieces" are cut longitudinally the apical "eyes" will develop shoots, and the lateral and basal "eyes" will be inhibited. If the "seed pieces" are cut transversely all "eyes" will develop shoots of equal strength and size. The vigor of the initial shoot growth is dependent upon the stored food material and the available auxin supply.

Murneek (44) has shown that there is a correlation between vegetative growth and fruit development in the tomato and other plants. If flowers are permitted to "set fruit",

vegetative growth is slowed down proportionally to the number of developing fruits. Pearsall (46), studying the correlative growth of cotton plants, found that developing fruits check flowering as well as vegetative growth. These data show that vegetative meristems cannot successfully compete with developing fruit for the available food supply, although they do not explain how the fruits are able to monopolize these materials.

The experiments of Loomis (41) show an interesting correlation which seems to associate the enzymatic system of the plant with the activity of hormones. His experiments indicate that massed meristems are able to use simple organic forms of nitrogen and to condense these forms into highly complex protoplasm in the formation of new cells. The diffuse meristem, cambium, remained inactive when the content of soluble organic nitrogen was relatively high. Auxin paste, applied to the apex of the shoot stimulated the cambium, and its activity was accompanied by an immediate reduction of soluble organic nitrogen in the phloem. Nitrogen condensation appears to have been caused either by the auxin itself or through the stimulation of enzymes by the auxin.

Correlation appears to be intimately associated with the life processes of the plant. It is affected by rates and intensities of cell division, transmitted by hormones, in some instances at least, and related to the processes of translocation of food materials and probably to the phloem mechanism.

MATERIALS AND METHODS

The plant materials used in these experiments consisted of seeds and seedlings of several varieties of corn: an open-pollinated strain of Iodent, a single-cross hybrid, several double-cross hybrids, and Hopi Indian corn. Iodent is a commercial variety developed by the Iowa Agricultural Experiment Station and commonly grown by Iowa farmers. Hybrid 420 x 426 the single cross hybrid was developed by the Farm Crops Department of Iowa State College in collaboration with the United States Department of Agriculture. Most of the experiments were performed with this corn. The Hopi Indian Corn is a drought-resisting variety grown by the Indians of southwestern United States, and generously supplied by the Arizona Agricultural Experiment Station. It is usually planted by the Indians in holes about a foot deep (43), and is known to develop long first internodes (21). In a preliminary experiment Hopi corn was grown ten days in complete darkness. The seedlings developed first internodes averaging 280 mm. in length (Fig. 1).

Plants were usually grown in six inch pots using a one to two mixture of fine sand and potting compost. In all experiments in which observations were made on the roots, sand was used as the potting substrate. Seeds were usually soaked in tap water two hours and then allowed to germinate 48 hours

between sheets of wet filter paper in a moist-chamber. Hopi corn was ill adapted to this method of treatment and had to be planted immediately after soaking. The primary radicle developed so rapidly during germination that the seeds could not be conveniently handled (Fig 2). The seeds were planted 5 mm. beneath the surface of the soil unless otherwise stated. Plants were removed from pots and measurements taken eight to ten days after planting. All operations, unless otherwise stated, were carried on in a photographic dark room at a temperature of 29 - 31° C, and dark plants were observed only by photographically safe light with minimum exposure even to this.

One hundred, three hundred, and five hundred watt Mazda lamps were used as sources of light in testing the effects of Mazda light. In all cases the plants were grown at a sufficient distance from the light bulbs to prevent heating. Eveready metal-core "Super-tan" carbons were used in the arc-light irradiation experiments. The intensity of illumination was measured with a Weston illuminometer.

At harvest the seedlings were thoroughly washed, blotted dry and cut with a razor blade at the base of the first internode as close to the scutellum as possible. Dry weights were obtained after drying 24 hours in an electric oven at 100° C.

The histological studies were made on materials fixed in Bouin's fluid, embedded in paraffin, and cut in microtome

sections 10 microns in thickness. Sections were stained with Mayer's haem-alum and counter-stained with saffranin (49).

The auxin paste used was a 1:400 mixture of indoleacetic acid and lanolin unless otherwise stated.

Throughout this paper the term "first internode" refers to that portion of the epicotyl between the scutellum and the coleoptile node (2, 14). Plumule is used primarily to designate the leaf meristem at the coleoptile node. Measurements of leaves are for foliage leaves only, but weights include the coleoptile as well.

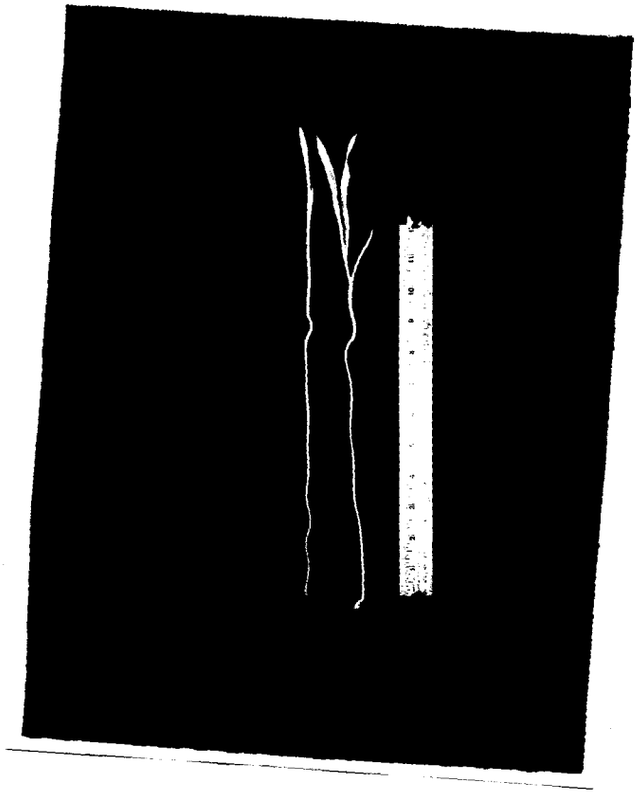

Fig. 1. Epicotyl development in Hopi Indian maize grown 10 days in the dark. Note the long first internode.

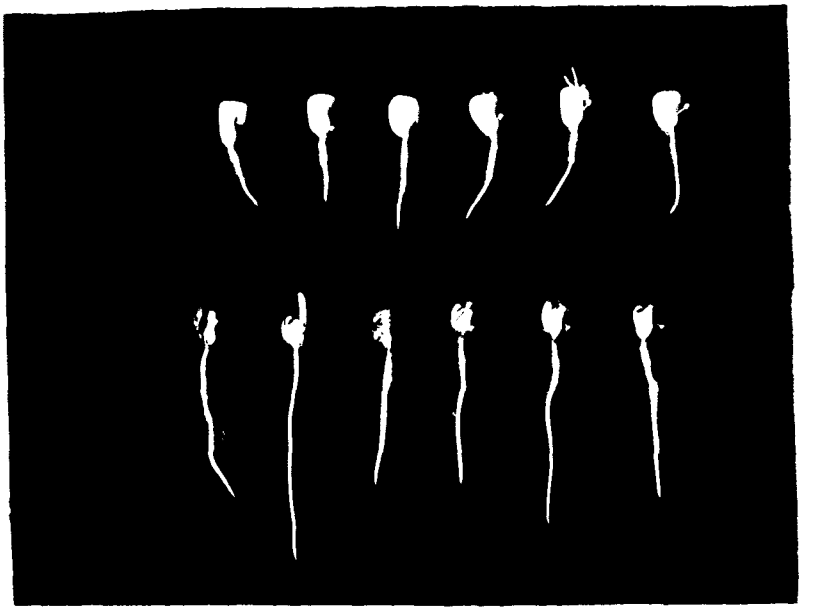

Fig. 2. Maize seeds after 48 hours germination in a moist chamber. 1. Upper row, hybrid corn with short radicles. 2. Lower row, Hopi Indian corn with long radicles.

EXPERIMENTAL RESULTS

Development of the First Internode of Maize Seedlings

The effect of Mazda illumination of varying intensity on first internode growth

Seeds were planted in pots and grown on a bench in a photographic dark room under constant exposure to light from a 100 watt Mazda lamp. The pots were arranged at varying distances from the source of light so that each pot received the indicated illumination (Table I). Each pot was leaned toward the light to give the entire surface of the soil a uniform illumination. Control plants were grown in a dark chamber in the same room.

First internode growth was checked very rapidly (Fig. 4) under comparatively low illumination. The curve has its maximum slope between 0 and 10 f.c., and a fairly steep slope between 10 and 30 f.c., while at higher intensities the slope is very gradual. The curves are practically the same for both varieties of corn used, although the hybrid corn was more susceptible to the influence of light than the Indian corn. In both cases (Table I) leaf growth showed a marked increase under the influence of the higher light intensities which effectively arrested the growth of the first internode. This experiment shows a negative correlation between leaf growth and first internode development. The light factors that

Table I. The effect of illumination of varying intensity on first internode growth. (Measurements made eight days after planting.)

Number of plants measured	Illumination in foot candles	Average length in mm.		
		First internode	Coleoptile	Foliage leaves
First Experiment - Hybrid corn used				
8	100	15.8	39.5	200.8
9	50	22.1	43.7	157.5
6	25	23.1	47.1	181.0
12	10	33.7	45.2	148.2
10	5	47.1	46.0	127.8
10	1	50.5	55.4	159.2
9	0 (Control)	71.7	52.6	92.8
Second Experiment - Hopi Indian corn used				
15	100	23.4	59.2	283.8
15	50	36.1	66.4	290.4
16	25	41.8	69.8	245.6
16	10	68.4	80.6	233.2
9	1	85.3	77.0	213.7
11	0 (Control)	166.5	111.7	197.0

retarded the growth of the first internode had a stimulating effect upon the plumule or else the check in first internode growth permitted the food supply to be diverted to leaf growth.

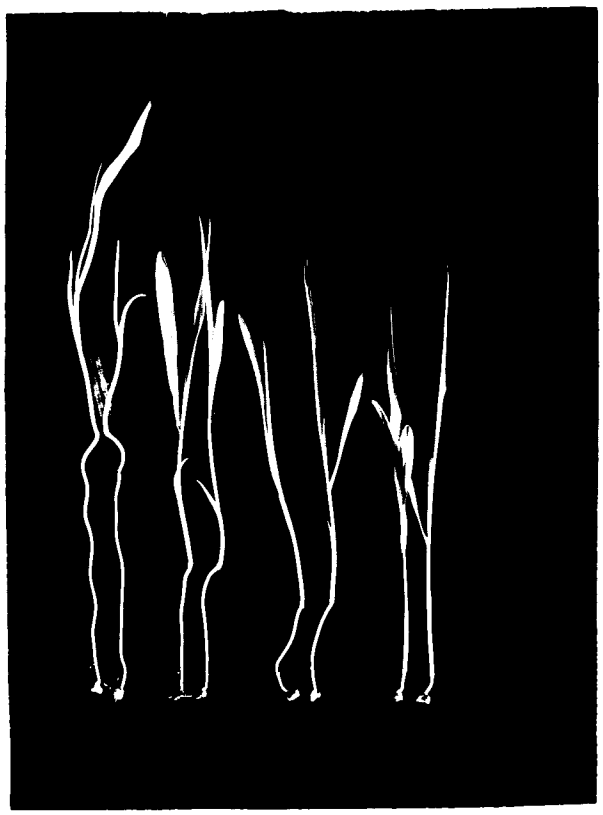

Fig. 3. The effect of illumination of varying intensity on first internode growth.

Left to right: (1) grown in dark, (2) grown at 1 f.c. illumination, (3) grown at 10 f.c. illumination, (4) grown at 100 f.c. illumination, Plants illustrated were from the experiment using Hopi Indian corn.

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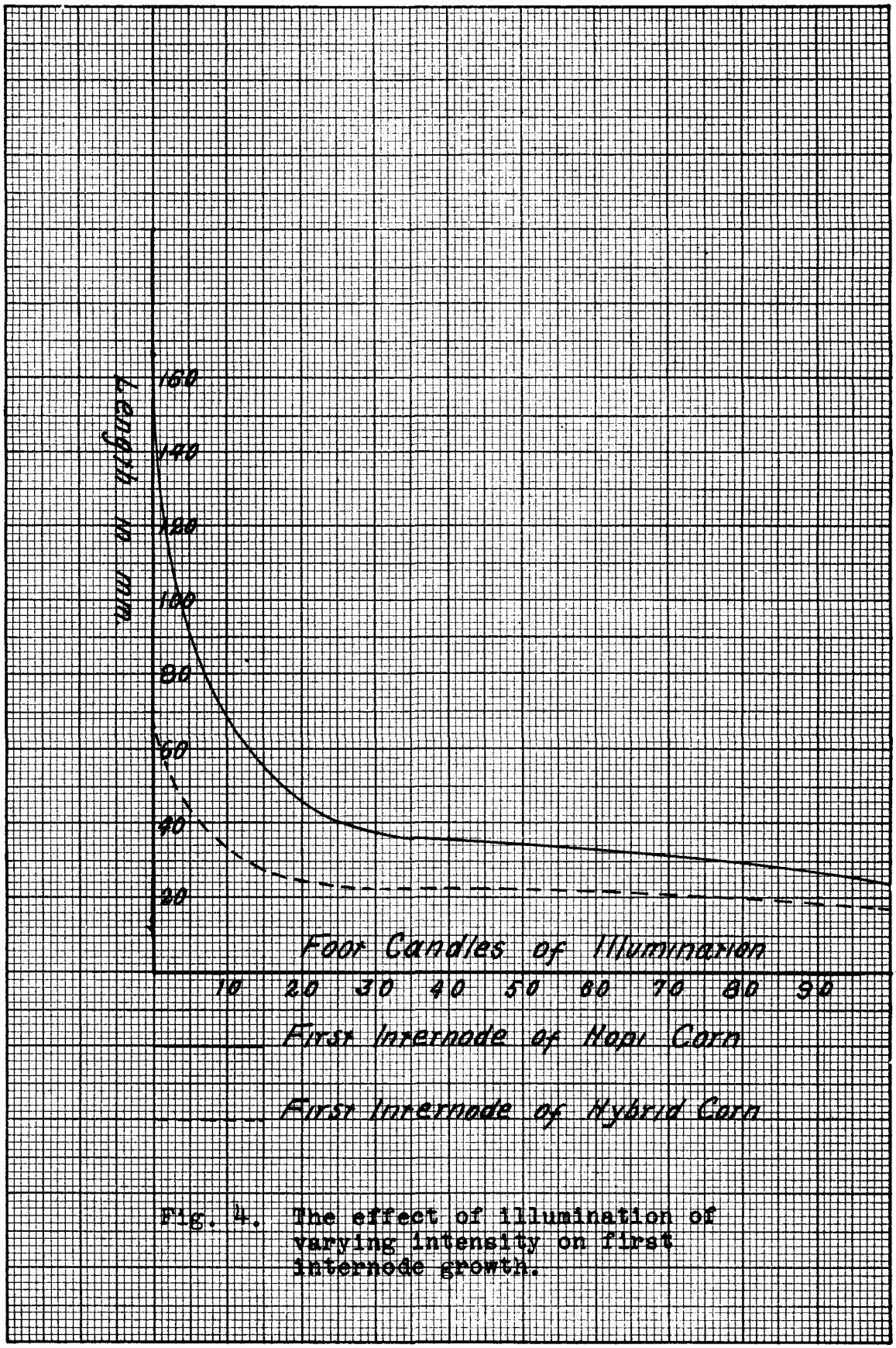

Fig. 4. The effect of illumination of varying intensity on first internode growth.

The effect of Mazda illumination of constant intensity for varying lengths of time on first internode growth

Hopi Indian corn was planted in pots and grown under 100 f.c. of constant illumination from a 300 watt Mazda lamp. At 24 hour intervals after the coleoptiles appeared above the surface of the soil, pots were removed from the light to the dark. Control plants were grown in the dark. All plants were removed from the pots 10 days after planting and measurements taken.

TABLE II. The effect of constant illumination of 100 f.c. for varying lengths of time on first internode growth of Hopi corn.

Hours illuminated	No. of plants measured	Average length in mm.		
		First internode	Coleoptile	Foliage leaves
0 (Control)	11	166.2	111.7	197.0
24	15	42.3	71.4	311.1
48	16	31.1	60.9	322.1
72	14	25.3	65.5	304.2
144*	15	23.4	59.2	283.8

Another experiment was performed in the same manner using hybrid corn, and cutting the time interval for removing the pots from the light to dark from 24 to 12 hours. Results are shown in table III. A weak illumination for a long period of time produced the same response in first internode growth as a strong illumination for a short period of time.

* This pot remained in light for the duration of the experiment.

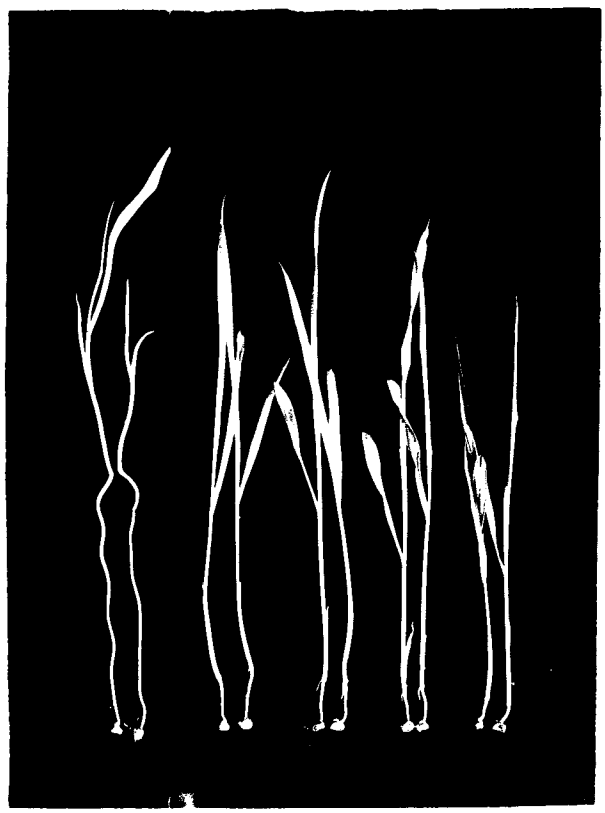

Fig. 5. Hopi Indian corn grown under constant illumination of 100 f.c. for varying lengths of time.

From left to right: (1) control grown in dark, (2) exposed to light 24 hours, (3) exposed to light 48 hours, (4) exposed to light 72 hours, (5) grown under constant light.

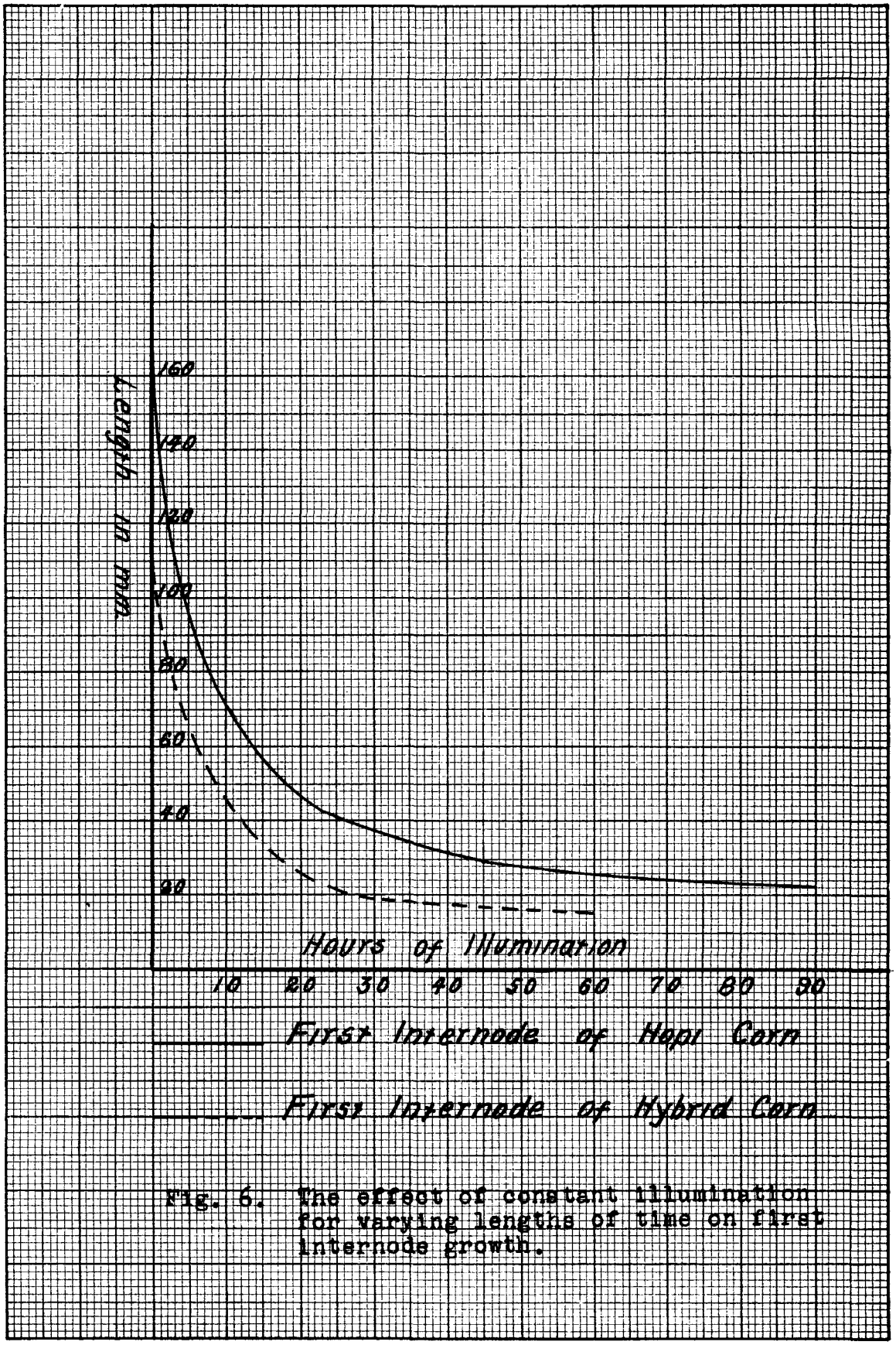

Fig. 6. The effect of constant illumination for varying lengths of time on first internode growth.

TABLE III. The effect of constant illumination of 100 f.c. for varying length of time on first internode growth of hybrid corn.

Hours illuminated	No. of plants measured	Average length in mm.		
		First internode	Coleoptile	Foliage leaves
0 (Control)	15	112.0	67.0	142.7
12	12	42.3	52.5	158.7
24	12	23.5	49.4	160.5
36	13	19.1	43.2	144.7
48	13	17.0	40.3	149.6
60	13	15.9	40.6	133.4

The effect on first internode growth of irradiation of coleoptiles with carbon arc light

Hybrid corn was planted in pots and allowed to grow until the coleoptiles were about 2.5 cm. above the surface of the soil. They were then irradiated with a metal-core carbon arc light at 300 f.c. intensity of illumination for varying lengths of time as shown in table IV. Three days after irradiation plants were removed from pots and measurements taken.

The growth of the first internode (Fig. 7.) was rapidly checked with short periods of irradiation. Under the same treatment the foliage leaves produced by the plumule showed an increase in growth which reached an optimum response in plants irradiated between 10 and 20 minutes. With longer periods of irradiation the plumule showed a steady decline in growth. This loss was probably due to protoplasmic injury brought about by the high content of ultra-violet rays in the arc light.

TABLE IV. The effect of arc light irradiation on first internode growth.

Time of exposure (min.)	No. of plants measured	Average length in mm. First internode	Coleoptile	Foliage leaves	Av. wt. of seedlings in mg. Fresh	Dry
0 (control)	12	78.5	60.7	85.4	841.6	41.7
1	12	72.6	61.0	85.0	905.0	47.7
10	11	51.6	57.8	110.3	1000.0	51.6
20	10	45.6	52.0	111.6	870.0	44.8
40	11	40.7	49.0	95.5	720.0	39.4
80	9	38.7	40.0	78.4	555.0	32.4

It is interesting to note that the maxiumum growth occurred in plants that were irradiated with the arc light for 10 minutes. This short light exposure appears to have significantly increased translocation from the seed, as measured by average dry weight of seedlings.

The effect on first internode growth of irradiating germinating seeds with sunlight and with arc light

Iodent and hybrid corn seeds were germinated 48 hours between sheets of wet filter paper in a moist chamber. In most cases the seed coats were ruptured and the radicles had begun to emerge. Half of the Iodent seeds were placed in a dish of wet moss and irradiated 45 minutes with metal-core carbon arc light at 300 f.c. intensity. They were then planted and grown in the dark with the untreated controls. The hybrid seeds were put on a wet filter paper in a glass dish and exposed to direct sunlight for eight hours, after which they were planted and grown in the dark with non-irradiated plants as controls. Five days later the plants were removed from the pots and measurements taken.

The data are conflicting and the differences in response of irradiated and non-irradiated seeds were not significant. Several workers (15, 17, 29) have reported that growth of the first internode in Avena is checked by exposing seeds to bright illumination during the "soaking period." Evidently corn is not as responsive to this treatment as oats.

TABLE V. The effect on first internode growth of irradiating swollen seeds with arc light and sunlight.

Kind of corn	Treatment	Plants measured	Average length in mm. First internode	Coleoptile	Foliage leaves
Iodent	Irradiated 45 min. with arc light	23	62.4	52.0	180.7
"	Non-irradiated	20	69.7	52.5	190.3
Hybrid	Irradiated 8 hrs. with sunlight	16	145.8	74.0	105.5
"	Non-irradiated	14	141.4	70.0	98.6

The inhibition of first internode growth by decapitation of the coleoptile

Hybrid corn seeds were planted in pots in the usual manner and grown in the dark. Two days after planting, when the coleoptiles had emerged 2.5 cm. above the surface of the soil, 2 mm. of the coleoptile tips was removed; six hours later a 1 mm. section was removed, and twelve hours later the tips were again decapitated. Untreated control plants were grown. Three days later the plants were removed from the pots and measurements taken. The data are recorded in table VI.

Decapitation of the coleoptile tips reduced the growth of the first internode nearly 50 per cent under the control (Fig. 8). The growth of the coleoptile at the same time was effectively reduced. Leaf growth suffered from the

TABLE VI. The inhibition of first internode growth by decapitation of the coleoptile.

No of plants measured	Treatment	Average length in mm. First internode	Coleoptile	Foliage leaves
14	Tips uncut (Dark control)	97.9	66.5	103.5
14	Coleoptiles decapitated 3 times	56.4	44.0	87.4

decapitations and did not show the stimulation which might have been expected. The successive decapitations prevented the physiological regeneration (15, 24, 40) of the coleoptile tip.

A second experiment was performed in which hybrid corn was used. The seeds were planted in pots as usual. One pot was grown under 75 f.c. constant illumination and another pot was grown in the dark. After the dark grown plants had emerged 2.5 cm. above the surface of the soil, the entire coleoptiles were removed from a number of plants, with as little damage as possible to the plumule leaves. Four days later the plants were removed from the pots and observations made.

It will be observed (Fig. 9) that removal of the entire coleoptiles reduced the growth of the first internode almost to the level of the light grown controls. The data from these experiments seem to indicate that growth of the first internode and coleoptile growth are positively correlated and dependent upon a supply of auxin from the coleoptile tip.

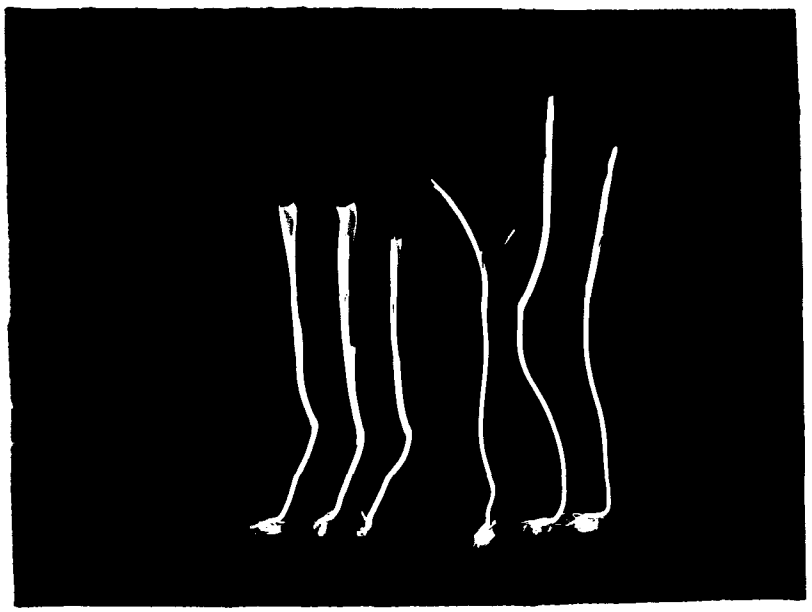

Fig. 8. The effect of decapitation of coleoptiles on first internode growth.

The first internodes of the plants on the left have been reduced nearly 50 per cent by three decapitations of the coleoptiles. The control plants on the right grew normally. All plants in dark.

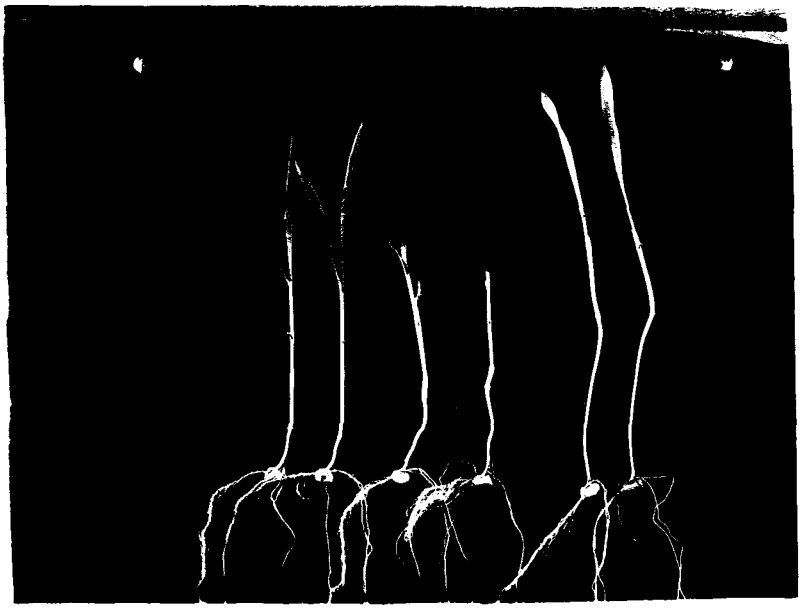

Fig. 9. The inhibition of first internode growth by complete removal of the coleoptile.

Left to right: (1) light controls grown under 75 f.c. illumination, (2) dark grown plants showing inhibition of first internodes by removal of coleoptiles, (3) dark controls showing long first internodes when coleoptile was undisturbed.

The effect of the interaction of auxin and illumination on first internode growth

Hybrid corn seeds were planted in pots in the usual manner and grown in the dark. Two days after planting, when the coleoptiles had emerged about 2 cm. above the surface of the soil, one of the pots was exposed to daylight for seven hours during two hours of which time the plants were in direct sunlight. At the end of the exposure the coleoptile tips were cut from half the plants in the exposed pots, and auxin paste was applied to the decapitated stumps. The plants were returned to the dark chamber and allowed to grow for three days. They were then removed from the pots and measurements taken. The data are recorded in table VII.

TABLE VII. The effect of auxin in preventing first internode inhibition after exposure of plants to daylight.

No. of plants measured	Treatment	Average length in mm.		
		First internode	Coleoptile	Foliage leaves
14	Tips uncut (Dark control)	97.9	66.5	103.5
6	Daylight 7 hrs., tips cut and auxin applied	61.5	80.8	---- *
8	Daylight 7 hrs., no auxin applied (Light control)	37.0	56.9	96.6

* Leaves had not emerged from the elongated coleoptiles.

It will be observed that the seven hour exposure to daylight arrested the growth of the first internode and that this inhibition was largely overcome by the applied auxin. The growth of the coleoptiles of the auxin treated plants was especially stimulated and far exceeded that of the controls.

A second experiment was performed with Hopi Indian corn. The plants were grown under 100 f.c. illumination and control plants were grown in the dark. Twenty-four hours after the coleoptiles of the plants in the light appeared above the surface of the soil, the uncut coleoptile tips of half the plants in two pots were treated with auxin paste. One of the pots was placed in the dark and the other remained in the light for the duration of the experiment. Two days later half the plants in another illuminated pot were treated with auxin paste and the pot transferred to the dark. Plants were removed from the pots and measurements taken ten days after planting.

In all cases, irrespective of the length of exposure to light, the first internodes and coleoptiles of the auxin treated plants were longer than those of the untreated plants in the same pot (Table VIII). It will also be observed that the foliage leaves of the auxin treated plants (Fig. 10) were uniformly shorter than those of the untreated. The auxin paste was applied to the intact coleoptile tips and coleoptile elongation was stimulated to a greater extent than first internode elongation. Even when the paste was applied promptly at the end of the first 24 hour exposure to light it was

relatively ineffective in stimulating internodal growth. When the auxin application was delayed 72 hours the effects were very small although still observable.

When plants were germinated in darkness and then illuminated for 24 hours at 100 f.c. with auxin paste applied three times to decapitated coleoptiles at 12 hour intervals, beginning at the time the plants were transferred to the light, the effects of the auxin were marked and very largely neutralized the modifying action of light (Fig. 11). These results suggest that the stage of first internode elongation and plumule inhibition is dependent upon auxin, but that once the shift from internode to plumule growth has been made it becomes largely irreversible.

TABLE VIII. The interaction of auxin and illumination of first internode growth. (Hopi corn used).

Hours exposed	Treated: Plants measured	Treated: Average length in mm. First internode	Treated: Coleoptile	Treated: Foliage leaves	Untreated: Plants measured	Untreated: Average length in mm. First internode	Untreated: Coleoptile	Untreated: Foliage leaves
0 (Control)					5	129.8	96.6	138.4
24	14	35.7	129.0	170.0	9	32.2	92.5	202.7
72	10	23.3	88.6	231.4	9	19.7	71.4	262.0
144	11*	20.5	106.2	254.0	10	16.7	67.0	286.2

* Treated plants in this group received auxin paste at the end of 24 hours in light.

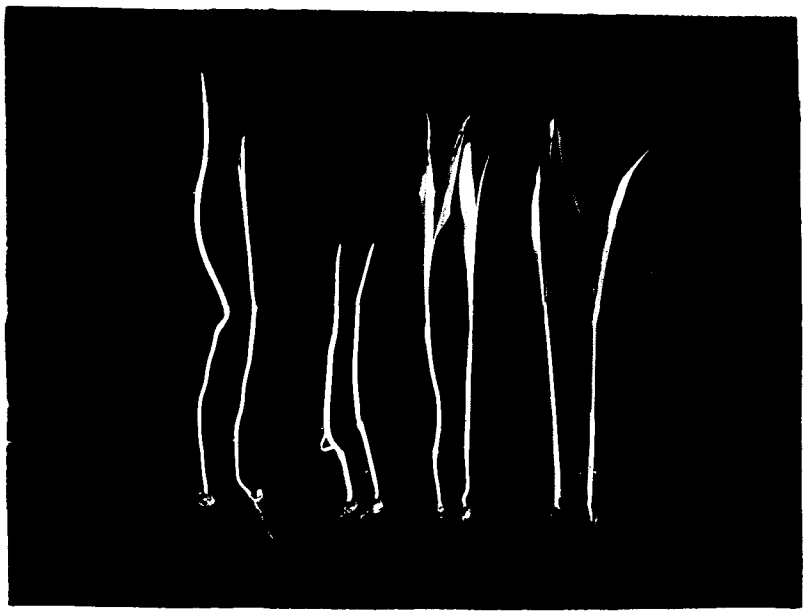

Fig. 10. The action of auxin in reducing the inhibition of first internode growth by light.

Left to right: (1) Control plants grown in dark, (2) plants in light 24 hours, treated with auxin and put in dark, (3) plants grown in light 24 hours, untreated and put in dark, (4) plants untreated and grown constantly in light.

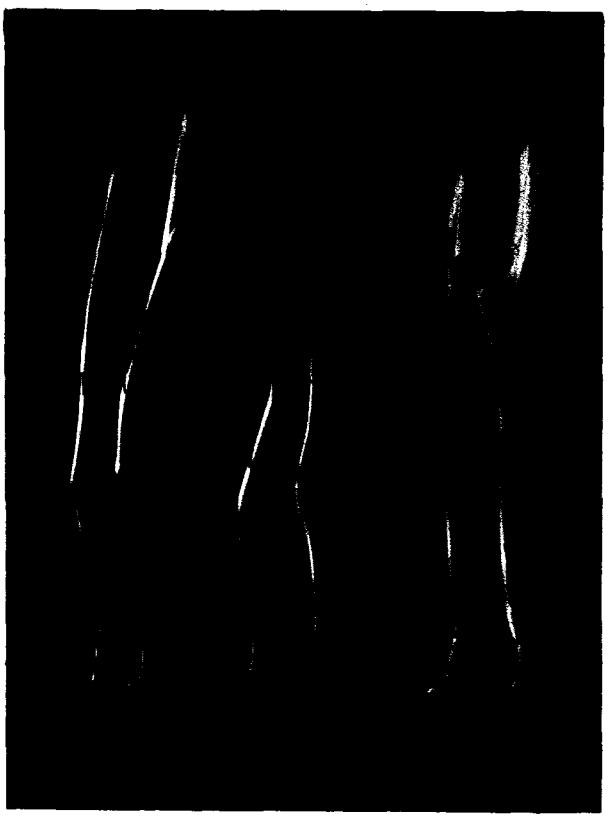

Fig. 11. The effect of light and auxin on development of first internode.

Left to right: (1) Control grown in dark throughout experiment, (2) grown 24 hours at 100 f.c. with auxin and 4 days in dark with auxin, (3) grown 24 hours at 100 f.c. and 4 days in dark, no auxin applied.

Other Growth Correlations

The effect of removal of tops on the growth of seminal roots

Hybrid corn seeds were planted in the usual manner and grown under 75 f.c. illumination from a 100 watt Mazda lamp. Two days later, when the coleoptiles had emerged about 2 cm. above the surface of the soil, the tops were removed from half the plants in the pot by cutting with a razor blade just below the coleoptile node, and the first internode stumps were covered with vaseline. Seven days later the plants were removed from the pots and observations made on the roots.

TABLE IX. The effect of removal of tops of hybrid corn on the growth of roots.

Treatment	No. of plants	Average wt. of roots in mg.	
		Fresh	Dry
Cut plants	10	614	85
Normal plants	11	465	47

A second experiment was performed with Iodent corn. Two pots were grown in the dark and another two pots grown under 75 f.c. illumination. Two days later the tops were removed from half the plants in each pot and the first internode stumps covered with vaseline as in the preceding experiment. Seven days later the plants were removed from the pots and observations made on the roots. The data are recorded

in table X.

TABLE X. The effect of removal of tops of Iodent corn on the growth of roots.

Treatment	No. of plants	Average wt. of roots in mg. Fresh	Dry
Light grown			
Cut plants	10	1000	81
Normal plants	11	800	76
Dark grown			
Cut plants	10	740	79
Normal plants	10	460	44

It will be observed that in all cases there was little difference in the dry weights of the roots of the cut plants. The roots of the cut plants were uniformly larger than those of the normal plants. The roots of the normal light grown plants were larger than those of the normal dark grown plants. These data might be explained by assuming inhibition of root development by the hormone produced in the etiolated coleoptile, or they might indicate competition between roots and tops for some growth factor deficient in etiolated plants. A third experiment was devised to test these hypotheses.

Hopi Indian corn was planted in pots and grown under 100 f.c. illumination from a 300 watt Mazda lamp. Three days later, when the coleoptiles had emerged 2.5 cm. above the surface of the soil, the tops were removed from half the plants in each pot. Auxin paste, 1:300 indoleacetic acid

in lanolin, was applied to the first internode stumps in one of the pots, and plain lanolin was applied to the stumps of the cut plants in the other pot. Three successive applications of auxin paste at two day intervals were given the treated plants. All plants were removed from the pots 10 days after planting and observations made on the roots. The data are recorded in table XI.

TABLE XI. The effect of auxin paste applied to decapitated first internodes on the growth of roots. (Hopi Indian corn used.)

Treatment	No. of plants	Average wt. of roots in mg.	
		Fresh	Dry
Auxin treated			
Cut plants	8	1485	101
Normal plants	10	944	60
Non-treated			
Cut plants	8	1254	84
Normal plants	13	745	45

For unexplained reasons the auxin treated series made the best root growth. The percentage gains of the auxin treated cut plants over their controls, however, was not significantly different from the gains of the untreated cut plants. The data indicate that root growth was not inhibited by the auxin even at the relatively high concentration that was used. It appears that correlative root and top growth in the early development of the seedling may be very largely a matter of competition for the available growth materials,

although the nature of these materials is not indicated. The consistently better root growth in plants illuminated at an intensity which unpublished experiments have shown to be at or below the compensation point for maize suggests that added synthesis of secondary growth factors may be involved and further work will test this possibility.

The effect of illumination on the development of roots at the coleoptile node

Hybrid corn seeds were planted in the usual manner and grown in the dark. Two days after planting, when the coleoptiles had emerged 2.5 cm. above the surface of the soil, the plants were exposed to 100 f.c. Mazda illumination for periods of time as shown in table XII, and returned to the dark to grow. Control plants were kept in the dark throughout. Freehand sections were made of the coleoptile node of several plants in each pot 48 hours after exposure to light. No root primordia were observed in the dark controls or in the plants exposed for 5 minutes. Root primordia had begun to develop in all of the other plants. Three days later the plants were removed from the pots and measurements taken.

It will be observed that at the end of the experiment (Table XII) the plants exposed 5 minutes had made more than half as much root growth as the plants exposed for 24 hours, and nearly four times as much as the dark controls. These

data indicate that only a short exposure to light was necessary to start the development of roots at the coleoptile node. At the same time root development, as indicated by the average total root length, increased with added illumination up to the maximum used.

TABLE XII. The effect of 100 f.c. Mazda illumination on the development of roots at the coleoptile node.

Time of exposure	No. of plants measured	Ave. no. of nodal roots	Ave. length of nodal roots in mm.	Ave. total length of roots of mm.
None (control)	36	1.0	1.0	1.0
5 Minutes	22	2.1	1.7	3.6
30 "	23	2.4	2.0	4.8
3 Hours	22	2.9	2.0	5.8
24 "	37	3.0	2.2	6.6

For histological studies of the development of roots at the coleoptile node, hybrid corn seeds were planted in pots in the usual manner and grown in the dark. Three days later one of the pots was exposed to 100 f.c. illumination from a Mazda lamp for 24 hours and returned to the dark. Two days later coleoptile nodes from both the light exposed and dark grown plants were fixed in Bouin's fluid and prepared sections made for study.

Root primordia were present in some of the dark grown plants (Fig. 12, 13), but had not begun active growth. In the light exposed plants, however, the root primorida were rapidly growing and ready to break through the epidermis to the outside (Fig. 14, 15).

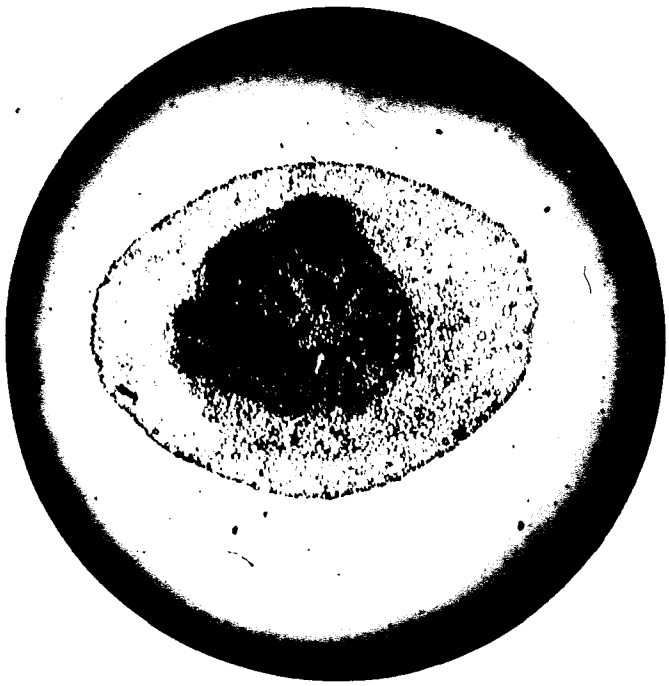

Fig. 12. Cross-section of coleoptile node. Plant grown six days in the dark.

Upper side of section shows two root primordia. Many of these plants showed no root development.

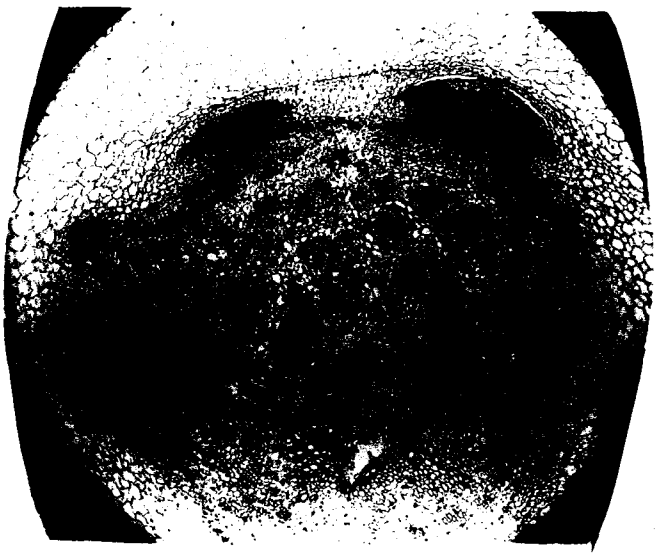

Fig. 13. Cross-section of coleoptile node. Plant grown six days in dark.

Same as Fig. 12 showing detail of nodal root primordia. The primordium to the right is beginning to show active growth.

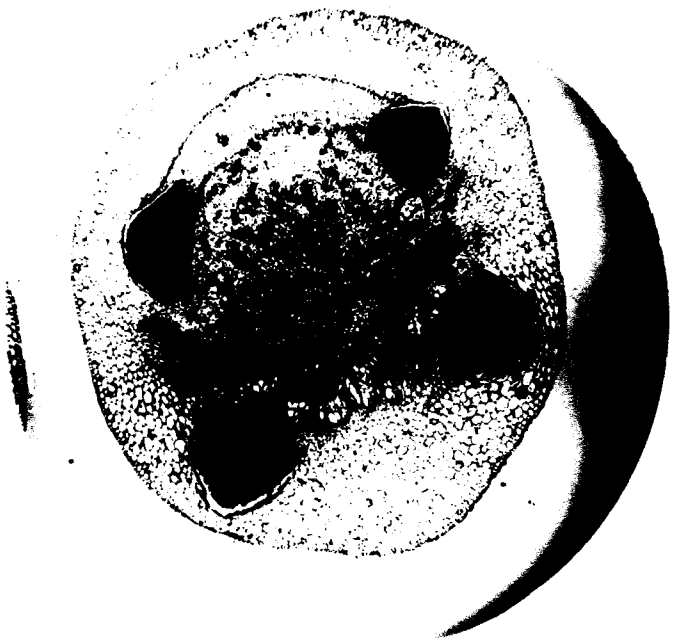

Fig. 14. Cross-section of coleoptile node. Plant grown three days in dark, transferred to light for 24 hours then in dark for 2 days.

Plant the same age as that of Fig. 12. Note the four well developed, actively growing root primordia. Note also the increased size of the node.

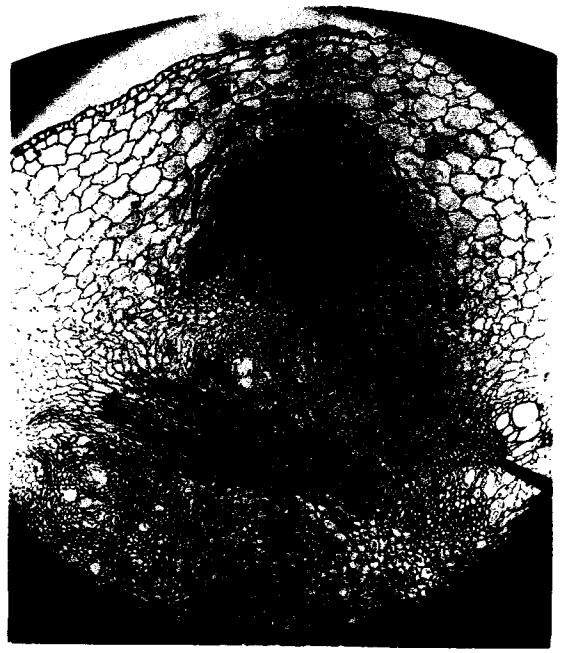

Fig. 15. Cross-section of coleoptile node. Plant grown three days in dark, transferred to light for 24 hours, and then put back in dark for 2 days.

Same as Fig. 14 showing detail of rapidly growing nodal root primordium.

Growth correlations in seedlings under different light treatments

Hybrid corn seeds were planted in pots in the usual manner and grown in the dark. Two days after planting, when the coleoptiles had emerged 2.5 cm. above the surface of the soil, 10 pots were irradiated with carbon arc light of 300 f.c. intensity seven times, for 10 minute periods at three hour intervals, and returned to the dark chamber. Control plants were grown in the dark. Three days after treatment all plants were removed from the pots and measurements taken. The data are recorded in table XIII.

At the end of the experiment only 12 of the control plants had developed nodal roots, and in no case were these roots more than 1 mm. long. Only 9 of the irradiated plants had not developed nodal roots;on practically all plants the nodal roots were from 5 to 10 mm. in length.

It will be observed (Table XIII) that the light treatment checked the growth of the first internode, but stimulated growth of the foliage leaves and roots. It appears that light through its action on some factor in the coleoptile tips had a definite stimulating affect on root growth.

A second experiment was performed in which hybrid corn seed was planted in pots and grown in the usual manner. The plants were treated in four series of 8 pots each. The first series was grown under 40 f.c. of constant Mazda

TABLE XIII. The effect of carbon arc light irradiation on growth of the seedling.

Treatment	No. of plants measured	Average length in mm.			Average weight in mg.							
		Foliage leaves	First internode	Roots	Leaves* Fresh	Leaves* Dry	First internode Fresh	First internode Dry	Roots Fresh	Roots Dry	Seed Fresh	Seed Dry
Dark grown (control plants)	139	67	128	154	393	31	483	33	509	45	474	139
Irradiated plants	125	143	47	178	667	32	198	15	534	50	415	120

* Includes coleoptile and coleoptile node.

illumination. The second series was irradiated with carbon arc light of 300 f.c. intensity 5 times for 15 minutes each at four hour intervals beginning two days after planting, and then grown in the dark. The third series was grown in the dark, and two days after planting the plants were exposed to 40 f.c. Mazda illumination for 12 hours, after which the Coleoptile tips were decapitated and auxin paste applied, and the plants returned to the dark chamber. Twenty-four hours later a second application of auxin paste was made. The fourth series remained in the dark chamber throughout the duration of the experiment. Ten days after planting all plants were removed from pots and measurements taken. The data are recorded in table XIV.

It will be observed that the growth of the first internode was effectively arrested under the low intensity of Mazda illumination used. The low intensity of Mazda illumination failed to stimulate root growth as had been observed in previous experiments under stronger illumination. The foliage leaves attained the best growth under the weak Mazda illumination.

Previous experience had indicated that the exposure to 40 f.c. for 12 hours was sufficient to stop internodal growth in a short time, yet these illuminated and auxin treated plants made practically the same internodal growth as the dark controls. It is interesting to note the slight differences in the total dry weights of the seedlings. The

TABLE XIV. Growth correlation in seedlings grown under different light treatments.

Treatment	No. of plants measured	Average length in mm.			Average weight in mg.							
		Foliage leaves	First internode	Roots	Foliage leaves		First internode		Roots		Seedling	
					Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
Mazda illuminated (light controls)	82	261	16	195	890	69	101	7	551	50	1542	126
C. -Arc irradiated	95	231	29	202	976	63	127	8	641	54	1744	125
Light + Auxin	93	149	113	217	852	58	365	26	584	53	1801	137
Dark grown (Controls)	91	170	121	206	887	54	331	24	532	45	1750	123

dry weights were essentially the same for all except the auxin treated plants. The distribution of dry weight in the auxin treated plants is about the same as in the dark controls. It appears that auxin not only accelerated growth of the first internode, but also increased translocation from the endosperm to all parts of the seedling; for the average dry weights of each part of the auxin treated plants exceeded those of the dark control.

The shift from internode to leaf growth is striking, and since total dry weight was not affected, represents a shift in the utilization of food materials. The data show quantitatively a relationship which has been observed throughout the study.

Root-leaf and root-top ratios in normal and etiolated seedlings

Root-top ratios show the correlative influences reciprocally exerted by the roots and aerial parts of the plant during its growth. Many factors both internal and external may influence the correlative growth of the over-ground and under-ground parts of the plant, but the ratios in seedling plants should be mainly influenced by competition for food from the endosperm and by directly inter-acting factors such as hormones and vitamins.

In this study the term "tops" is used to mean all parts of the seedling above the scutellum. "Root-top ratio" expresses the weight of the roots as a per cent of the weight of the tops. "Leaves" include the coleoptile and coleoptile node.

An initial tabulation was made of data from the series of plants described in the preceding experiment. The data are recorded in table XV.

Fresh weights, as stated above, are better indicators of growth and dry weights of translocation and differentiation. Although the leaves grew out more rapidly on the lighted, untreated plants the tops of the dark controls had nearly caught up with them by the time these plants were harvested. On the various bases the roots weighed from 44 to 76 per cent as much as the tops. The only significant differences in ratios were between the dark control and carbon-arc irradiated plants,

TABLE XV. Root-leaf and root-top ratios.

Treatment	No. of plants measured	Average weight in mgs.						Root-leaf ratio		Root-top ratio	
		Roots		Leaves		Tops					
		Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
Light Controls	82	551	50	890	69	991	76	62	72	56	66
C-Arc Irradiated	95	641	54	976	63	1103	71	66	86	59	76
Auxin Treated	93	584	53	852	58	1217	84	69	91	48	63
Dark Controls	91	532	45	887	54	1218	78	60	83	44	58

although there were indications of relatively poor root growth in the dark control and auxin treated plants, in both of which leaf growth was delayed if not greatly reduced and first internode growth stimulated.

Hopi Indian corn was used in a second experiment to determine more accurately the effect of light on root-top ratio and to determine whether the low ratios of the dark plants might increase after the leaves broke through the plumules as the result of lowered auxin production in the older coleoptile tips.

The seeds were planted in pots in the usual manner, and half the plants were grown under 100 f.c. Mazda illumination and the remainder grown in the dark chamber. The plants were removed from the pots and measurements taken at time intervals up to eight days as noted in table XVI. The average weights of the leaves, including the coleoptile and coleoptile node, the first internodes, and roots were calculated also as percentages of the average weight of the seedlings. These data are recorded in table XVII.

It will be observed (Table XVI) that there was a rapid increase in leaf growth in the dark grown plants after the fourth day. There was an early inhibition of root growth which reached a maximum on the fifth day. Thereafter accelerated leaf growth was accompanied by relatively greater root growth. The root and leaf growth of the light grown plants were fairly uniform after the third day. The first internode of the light

TABLE XVI. Root-top ratios.

Treatment	No. of plants measured	Average weight in mgs.						Root-leaf ratio x 100		Root-top ratio x 100	
		Leaves		First internode		Roots					
		Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
Three days after planting											
Dark Plants	9	97	14	189	16	154	14	159	100	54	47
Light Plants	10	153	17	92	9	196	19	128	112	52	73
Four days after planting											
Dark Plants	10	276	24	321	22	222	21	80	88	37	46
Light Plants	10	400	35	102	9	297	25	74	71	59	57
Five days after planting											
Dark Plants	10	447	30	488	25	266	20	60	67	28	36
Light Plants	10	552	43	80	6	478	31	87	72	76	63
Six days after planting											
Dark Plants	10	733	56	412	25	430	26	59	46	38	32
Light Plants	9	886	70	89	6	758	46	86	66	78	61
Eight days after planting											
Dark Plants	10	1220	91	328	19	774	41	63	45	50	37
Light Plants	10	1146	98	80	6	890	54	78	55	73	52

TABLE XVII. Leaves, first internode and roots expressed as per cent of total weight of seedling.

Treatment	Weight of Seedling		Per cent leaves		Per cent first internode		Per cent root	
	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
Three days after planting								
Dark Plants	440	44	22.04	31.81	42.95	36.36	35.00	31.81
Light Plants	441	45	34.69	37.77	20.86	20.00	44.44	42.22
Four days after planting								
Dark plants	819	67	33.69	35.82	39.19	32.83	27.10	31.34
Light plants	799	69	50.06	50.72	13.09	13.04	37.17	36.23
Five days after planting								
Dark plants	1201	75	37.21	40.00	40.63	33.33	22.14	26.66
Light plants	1110	80	49.72	53.75	7.20	7.50	43.06	38.75
Six days after planting								
Dark plants	1575	107	46.53	52.33	26.15	23.36	27.30	24.29
Light plants	1733	122	51.12	57.37	5.13	4.91	43.73	37.70
Eight days after planting								
Dark plants	2322	151	52.54	60.26	14.12	12.58	33.33	27.15
Light plants	2116	158	54.15	62.02	3.78	3.79	42.06	34.17

grown plants had reached its maximum growth in the third day (Table XVII), whereas it continued to increase in the dark grown plants until the fifth day. These data suggest that the auxin factor that stimulates growth of the first internode in the dark also inhibits growth of the roots, and development of the leaves. It has been shown, however, that added heteroauxin has no effect upon root growth of decapitated seedlings, and the relationships involved are still obscure.

The condensation of nitrogenous compounds and the activity of apical and intercalary meristems

Hybrid corn seeds were planted in two flats and grown in the dark. Three days later, when the coleoptiles had emerged about 2.5 c.m. above the surface of the soil, one of the flats was exposed to 100 f.c. Mazda illumination for 24 hours. Half of the plants were then removed from each flat and both flats returned to the dark chamber and allowed to grow. The harvested plants were cut as rapidly as possible, killed in hot alcohol, and prepared for chemical analysis. The internode samples consisted of the entire first internode while the "plumule" samples included the leaves, coleoptile, and coleoptile node. The samples were extracted with 80 per cent alcohol (42), and soluble nitrogen was determined in aliquot samples of the extract by the kjeldahl method. Two days later the remaining plants were removed from the flats and chemical analysis made in the same manner. The data are

recorded in table XVIII.

TABLE XVIII. Changes in soluble nitrogen of seedlings illuminated 24 hours with 100 f.c. Mazda light.

Plant material	Mg. soluble N in 100 gm. of sample: Dark controls	Lighted plants	Difference
After 24 hours light.			
Internodes	154	200	+46
Plumules and coleoptiles	128	152	+24
48 hours later			
Internodes	166	209	+43
Plumules and coleoptiles	135	145	+10

The data show a rapid increase in the soluble organic nitrogen of the seedlings exposed to the light, particularly in the internode tissues, although the opposite effect might have been expected. This increase paralleled the shift from the growth of the internode to rapid development of the massed meristems of the plumule and nodal roots. Loomis (41) has assumed that diffuse meristems, such as the intercalary meristem responsible for first internode growth, are relatively ineffective in building soluble organic nitrogen compounds into protoplasm unless stimulated by auxin or other factors. The data may be explained by assuming that a continued supply of hormone from the coleoptile tip not only inhibits directly the growth of the massed meristems (25, 68) but also catalyzes the condensation reactions which make intercalary division possible. With the failure of this auxin supply from the

illuminated coleoptiles (17) soluble organic nitrogen compounds accumulated and were utilized by the massed meristems; the accumulation itself perhaps being a stimulating factor.

A second experiment was run with hybrid corn to observe the changes in soluble nitrogen at the time of the failure of coleoptile auxins with aging.

The plants were grown in flats as before. The light exposed plants were grown constantly under 100 f.c. Mazda illumination and the second flat grown in the dark. Half the plants were removed from the flats and chemical analysis made five days after planting. The remainder of the plants were removed four days later and chemical analyses made. The data are recorded in table XIX.

TABLE XIX. Changes in soluble nitrogen of seedlings grown under constant 100 f.c. Mazda illumination.

Plant material	Mg. soluble N in 100 gm. of sample: Dark controls	Lighted plants	Difference
Five days after planting			
Internodes	184	229	+45
Plumules and coleoptiles	202	365	+163
Four days later			
Internodes	104	83	- 21
Plumules and coleoptiles	152	114	- 38

The first samples, taken when the plants were well up, contained even greater accumulations of soluble nitrogen in the lighted plants than were shown in Table XVIII. Samples taken

nine days after planting, however, showed sharp drops and a reversal of the two groups in their soluble nitrogen percentages. The etiolated plants had shifted to leaf and nodal root growth by this time and only the 100 f.c. lighting was present as a variable. Under these conditions the direct condensing effect of light (41) became dominant. The decreases in soluble nitrogen in both the dark and lighted plants may be attributed to partial endosperm exhaustion.

DISCUSSION OF RESULTS

The data from these experiments show that there is a positive correlation between growth of the first internode and growth of the coleoptile, and a negative correlation between first internode growth and development of the plumule. Auxin appears to be the main factor influencing these correlations. Auxin formed in the coleoptile tip (76) stimulates growth of the coleoptile and first internode and inhibits growth of the apical meristem. Many data indicate that auxin in the coleoptile tip may be destroyed or inactivated by light. In the normal growth of maize seedlings, as soon as the coleoptile reaches the surface of the soil the auxin supply from the tip is reduced by light and the elongation of the first internode stops. Plumule growth is immediately accelerated. Hetero-auxin paste applied to the coleoptile during or immediately after an exposure to light sufficient to cause this growth shift, in a large measure nullified this effect of light. First internode growth was inhibited also by a complete removal of the entire coleoptile or by several successive decapitations of the coleoptile tip. In every case where first internode growth was inhibited, regardless of the method used, plumule growth was stimulated.

Growth of roots at the coleoptile node was positively correlated with plumule growth. Any exposure to light of sufficient intensity to check first internode growth and

accelerate plumule growth also stimulated growth of roots at the coleoptile node. Histological studies showed that nodal root primordia became active in dark grown plants after four or five days of growth without exposure to light. Internode growth stopped and plumule development became active at the same time. It appears that after about five days growth in the dark at room temperature, either the auxin precursor (15, 48) in the endosperm became exhausted, or the aging coleoptile tip became inactive, resulting in a decreased auxin supply and a shift in growth from first internode to plumule without outside stimulation. Presumably added auxin would delay this shift. Once made this change in growth, regardless of the cause, was largely irreversible, apparently because of the differentiation of the cells of the intercalary meristem.

Kny (37) reported that root and top growth in seedling development were not correlated and that roots developed independently of the tops. The data from these experiments show that there is a competition for food material between roots and tops. Darkness seemed to favor top growth especially, of course, internode growth. Root development was apparently influenced by some factor, other than auxin, associated with the influence of light on the tops. Root growth was not inhibited by the application of auxin paste of a relatively high concentration to decapitated first internode stumps.

It was observed that plants grown in the dark and plants grown under various light treatments had essentially the same total dry weights. It appears that light did not influence translocation of food materials from the endosperm, but was rather a factor in determining the place where the food materials, were used. Auxin paste applied to the tips of decapitated coleoptiles apparently increased translocation from the endosperm. Auxin treated plants were usually larger than dark controls but the proportional distribution of growth was essentially the same.

Analyses of etiolated and illuminated plants indicate that the diffuse meristem of the first internode cannot readily convert simple organic nitrogenous compounds into the complex protein molecules of protoplasm without the aid of a continuous supply of auxin. The massed apical meristem does not need auxin to insure utilization of soluble organic nitrogen. The presence of auxin does, however, seem to inhibit apical growth. The abundant supply of auxin during the early development caused a rapid utilization of soluble organic nitrogen by the diffuse meristem of the first internode which resulted in growth. At the same time differentiation of the cells of the diffuse intercalary meristem region was prevented or delayed.

SUMMARY

Iodent, Hopi Indian and several strains of hybrid corn were used in studies of the distribution of maize seedling growth among the coleoptile, plumule, first internode of the epicotyl and the roots.

Illuminating the coleoptile tip resulted in a sharp shift from internode to leaf and nodal root growth. The addition of indoleacetic acid pastes at the time of illumination neutralized the effect of the light.

Shorter periods of high light intensity were as effective as longer periods of low intensity. Exposures of five minutes at 100 f.c. significantly affected the correlative development of maize seedlings. 100 f.c. for 24 hours gave complete and irreversible stoppage of first internode growth. Irradiation from a sunshine carbon arc was somewhat more effective than irradiation from a Mazda lamp.

Irradiation of germinating seeds did not affect the subsequent growth of the seedlings.

First internode growth was effectively inhibited by three decapitations of the coleoptile tip at four hour intervals or by complete removal of the coleoptile from seedlings grown in the dark.

In all cases in which growth of the first internode was inhibited plumule growth was stimulated. The same factors

that stimulated first internode growth also inhibit growth of the plumule and roots at the coleoptile node.

Light did not influence the translocation of food materials from the endosperm or total growth of seedlings, but affected the distribution of growth.

Correlations between roots and tops of seedlings were less striking. Root growth was moderately depressed during the period of rapid auxin activation by the coleoptile, but was not reduced by high concentrations of indoleacetic acid applied to the internode stumps as a paste. Decapitation in the first internode increased root growth of seedlings in either dark or light, but normal plants in light at 100 f.c. consistantly made a better root growth than the dark controls. The difference is not considered to be due to photosynthesis.

Plants showing internode growth were low in soluble organic nitrogen while plants of the same age, the growth of which had been shifted, were low in this fraction.

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